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A Name for the Poison Frog of Cordillera Azul, Eastern Peru, With Notes on Its Biology and Skin Toxins (Dendrobatidae)

CHARLES W. MYERS[1] AND JOHN W. DALY[2]

ABSTRACT

Dendrobates silverstonei, new species, is a distinctive orange-and-black or red-and-black frog discovered in the 1940s, as a consequence of road construction across the Cordillera Azul on the Amazonian flank of the Peruvian Andes. A colored photograph of a nurse frog, engaged in the dendrobatid trait of tadpole carrying, was widely promulgated in the multilingual editions of Cochran's *Living Amphibians of the World*, as well as in other popular works. The species is now removed from consideration with *Phyllobates bicolor*, the only frog with which it has been previously confused or seriously compared. The newly named *silverstonei* belongs to a group containing the type species of *Dendrobates* rather than to the demonstrably monophyletic group containing the type species (*bicolor*) of *Phyllobates*. The color pattern of *D. silverstonei* is a convergent autapomorphy showing only the most superficial resemblance to that of *P. bicolor*, and *silverstonei* lacks the potent batrachotoxin alkaloids of *Phyllobates*. Skin secretions contain small amounts of alkaloids, mainly of the pumiliotoxin-A class. *Dendrobates silverstonei* is placed tentatively in a species group containing *D. trivittatus*, because of similarities in morphology and natural history.

The highland *Dendrobates silverstonei* (above 1300 m. elevation) shares various biological attributes with the widespread lowland *D. trivittatus* (below 800 m.), and their nearly identical songs are described as *retarded trill calls*, the fourth class of dendrobatid vocalizations to be defined. Both species are wary and usually quick to hide, and both seem to have some preference for edge situations. Similar-sized clutches of eggs of each species have been found in dead leaves on the forest floor, with male frogs in attendance. Tadpoles are carried to terrestrial water by the male nurse frog. There is interpopulational variation in the color pattern of *D. silverstonei*, and perhaps also in the ontogenetic development of the pattern. Geographic variation is likely to be extensive if the species proves to occupy a large range in the montane forest of Cordillera Azul.

INTRODUCTION

The Cordillera Azul is one of the small mountain ranges that flank the eastern side of the high Andes. It stands between the northward-flowing Huallaga and Ucayali rivers, two major tributaries of the upper Amazon. It stands also between the towns of Tingo María

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and Pucallpa on the same rivers. In the 1930s, a road was brought down to Tingo María from the Andean highlands, thus allowing direct access by motor vehicle from Lima, and the effort was soon made to push the new road across the Cordillera Azul to Pucallpa on the Río Ucayali. This road crested a part of the range at a place known as La Divisoria, and then dropped through a formidable gorge—the Boquerón del Padre Abad—finally reaching Pucallpa sometime in the 1940s.

Travelers over the new road were a sparse but motley lot and included a few biologists, who quite naturally poked about in the newly accessible mountain forest near Divisoria. Their attention was sometimes drawn to a brightly colored orange-and-black or red-and-black frog of which one—possibly the first—was obtained in 1946 by John C. Pallister while on an entomological collecting trip for the American Museum of Natural History (Pallister, 1956). The specimen was duly recognized as a new species of dendrobatid frog and set aside for description by Emmett Reid Dunn, then a research associate in the Museum's Department of Amphibians and Reptiles. But the description never materialized (Dunn died in 1956) and the specimen languished in the unidentified collections until recently.

In the year following Pallister's trip, the collector José M. Schunke obtained a series of the frogs, which he sent to the Field Museum of Natural History. Nothing else seems to have happened until 1954, when a male frog with tadpoles on its back was caught and photographed by Edward S. Ross, an entomologist from the California Academy of Sciences. One of Ross's photographs was reproduced in color in a popular book by Cochran (1961). No other picture showing the curious sight of a frog carrying its tadpoles has been seen by so many people, owing to the huge success of Cochran's book and its translation into at least six languages. Unfortunately, Cochran misapplied the old name *Phyllobates bicolor* to the new frog, and almost everything said about it in the picture's caption is simply wrong. Photographs of the same specimen have been widely published in several other popular sources (*fide* Ross, *in litt.*), of which we have seen only one (Wenzel and Smith, 1971).

A few additional museum specimens were obtained in 1966 and 1971, by former Peace Corps biologist Wade C. Sherbrooke, and, in 1971, K. H. Lüling published some observations on the frog's natural history. Lüling's use of the name *Phyllobates bicolor* was evidently based on the German edition of Cochran's book, and such usage was foremost in our minds when we stated that the name *P. bicolor* "is currently applied to at least two different species of South American frogs" (Myers and Daly, 1971). The problem was more directly pointed out in 1976 by Philip A. Silverstone, who recognized that *P. bicolor* is confined to the northern Andes of Colombia and diagnosed the Peruvian frog as a doubtfully related and undescribed species. Silverstone refrained from naming the species in deference to our own ongoing work.

We had gone in search of the poison frog of Cordillera Azul in November 1974, although it proved to be a singularly bad time for travel. Because of the worldwide "energy crisis" of that year, even rental cars in Peru could be driven only on certain days of the week, and there was furthermore an acute shortage of fuel in the interior. We had but three "good" days, during which we worked along the gravel road and over the mountains as far as the Boquerón del Padre Abad. Time was short and the frogs were harder to find than we had anticipated, but we did acquire enough material to satisfy our curiosity about their skin toxins and we also gained some knowledge of their vocalizations, behavior and reproduction. This distinctive species has been nameless or misnamed for the three decades since its discovery, and we think it appropriate that it now be named after Dr. Philip A. Silverstone in recognition of his contributions to the taxonomy of dendrobatid frogs.

Dendrobates silverstonei, new species

Figures 1-4A,B, 5-8, 10B, 11-12

Phyllobates bicolor, not of Bibron: Cochran, 1961, color pl. 39 [reversed image of CAS 85151]. Cochran and Goin, 1970, pp. 35-37 (part: CAS 85151 only). Lüling, 1971, figs. 3, 5, 6 + color pl. Wenzel and Smith, 1971, p. 6 (color photograph [reversed image of CAS 85151]).

Phyllobates species: Silverstone, 1976, pp. 20-21,

frontisp. II (color painting [from transparency] of USNM 166904A), fig. 4F (outline drawing showing dorsal pattern of FMNH 56272).

[*Dendrobates*] species: Myers, Daly, and Malkin, 1978, p. 332 (generic assignment implied, removed from *Phyllobates*).

HOLOTYPE: AMNH 91844 (field no. CWM 12689), an adult male found by Charles W. Myers and John W. Daly on November 2, 1974, in montane forest of Cordillera Azul, 1330 meters elevation, apoximately 30 km. air line northeast of Tingo María, Department of Huánuco, Peru. This locality lies alongside the gravel road from Tingo María to Pucallpa, about 5 km. by road southwest of the road's crest at 1640 m. elevation.

PARATYPES: A total of 26 specimens, all from the Cordillera Azul in Department of Huánuco, Peru, as follows: AMNH 91845-91851, collected by the authors, November 3-5, 1974, at type locality. AMNH 94803-94805, 14-month-old frogs raised in captivity from eggs found attended by holotype at type locality. AMNH 53763, east slope Cordillera Azul at Divisoria, about 5000 ft. (John C. Pallister, December 1946). FMNH 56263-56272, Divisoria (José M. Schunke, August 1-7, 1947). AMNH 86493, 87924, 87925, Tea Gardens S.A., Río Azul, La Divisoria, about 1600 m. (Wade C. Sherbrooke, July 16-18, 1971). USNM 166904A, km. 189, FDO [Fundo] Íntimo [plantation near Divisoria], Tingo María-Pucallpa Rd., Provincia Leoncio Prado, about 1500 m. (Wade C. Sherbrooke, October 8, 1966). CAS 85151, 28 mi. NE Tingo María (Edward S. Ross, September 29, 1954).

Of the above specimens, AMNH 91847-91849 and FMNH 56265 are cleared and stained, and AMNH 87924 and 91850 are skinned carcasses. Paratypic larval and metamorphosing specimens are AMNH 94794-94802 (series of stages raised from eggs attended by holotype) and USNM 166904B (late larvae and metamorphosed froglets raised from dorsal tadpoles of USNM 166904A).

DEFINITION AND DIAGNOSIS: A large dendrobatid that attains a maximum snout-vent length of at least 43 mm. Head and body orange or red, with or without heavy spotting or marbling of black; no stripes; hind limbs all or partly black, with or without concealed calf spot. Teeth present on maxillary arch; appressed first finger slightly longer or equal to second; third finger disc about 1.2-1.6 times wider than finger. Piperidine skin alkaloids present, batrachotoxins absent.

Dendrobates silverstonei is readily differentiated from most other dendrobatids by the combination of large size and distinctive (albeit variable) color pattern lacking stripes. Specimens with uniformly bright-colored bodies su-

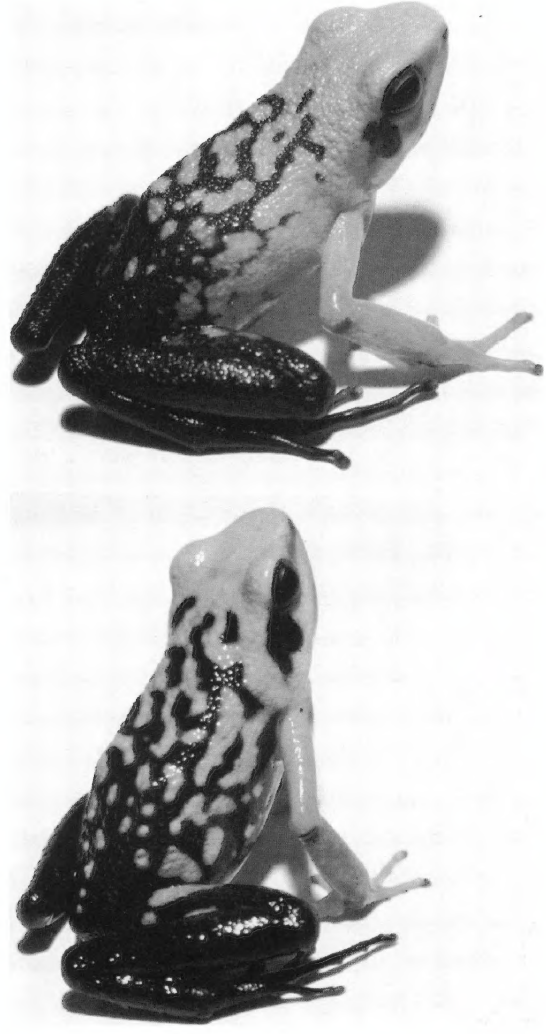

FIG. 1. *Dendrobates silverstonei*, new species, approximately ×1.6. *Top*: The adult male holotype (AMNH 91844) in life. *Bottom*: An adult female paratopotype (AMNH 91845).

perficially resemble the geographically remote *Phyllobates bicolor* (NW Colombia), but can be distinguished by the coarsely granular skin on the lower back of *D. silverstonei* (smooth in *P. bicolor*, but see p. 5n), more prominent foot tubercles (fig. 4), and by various other differences (see Systematics section).

MEASUREMENTS (IN MM.) OF HOLOTYPE: The male holotype (fig. 1, top) is sexually mature as shown by its fairly large size, opened vocal slits, and by the fact that it was tending a clutch of eggs when found. Length from snout to vent 38.3; tibia length from heel to fold of skin on knee 18.4; greatest width of body and greatest head width (between angles of jaws) both 11.5; head width between edges upper eyelids 10.1; approximate width of interorbital area 5.0; head length from tip of snout to angle of jaws 11.3; tip of snout to center of naris 1.3; center of naris to anterior corner of eye 3.6; distance between centers of nares 5.1; eye length from anterior to posterior corner 4.8; horizontal diameter of tympanum (posteriorly indistinct) about 2.5; corner of mouth to lower edge tympanic ring 0.8; length from proximal edge of large medial palmar tubercle to tip of longest (3rd) finger 11.3; width of disc of third finger 1.1; width of third finger (penultimate phalanx) below disc 0.8; width of discs of third and fourth toes both 1.4, and width of third and fourth toes below discs both 0.8.

DESCRIPTION OF ADULTS

Size large, with maximum observed snout-vent length of 42.8 mm.; females several millimeters longer than males on average (table 1). Widest part of head between jaw articulations. Head more or less as wide as body, except gravid females tending to be more rotund; head width averaging 99 percent of greatest body width in 12 males (range 87-115%) and 88 percent in six females (78-118%). Little external sexual dimorphism except in size. Adult males with shallow subgular vocal sac, rarely indicated externally by weak longitudinal crease (not a definite fold) on each side of throat; gular area often pigmented gray or black in females as well as males. Adult males with well-developed vocal slits on floor of mouth.

In life, orange, reddish orange, or red[1] on forelimbs, head, and body—often with black spotting, or with black reticulum extending forward on back, sometimes so extensively as to demarcate bright spots on a black ground (cf., figs. 2, 3). Individuals having extensive black on dorsum usually have tympanum concealed in black postocular spot, and, with addition of black preocular stripe, some have complete face mask; such individuals also may have black markings on forelimbs (fig. 2). Hindquarters black, with or without spots of body color on thighs, or with bright body color extending dorsally over thighs and onto shanks. Some specimens (e.g., holotype) with large calf spot of body color concealed below knee on anteroventral face of tibia, this mark reduced or absent in others, or present but fused with bright color from atop thighs in individuals having brightly pigmented limbs. Underside of head and body variably pigmented, ranging from black to nearly uniformly pale, faded orange (figs. 2, 3). In life, any light ventral color much paler and not as bright as on dorsum and often suffused with gray, except undersides of arms the same as above; palms and undersides

[1]We have not seen a living frog that is truly red, but it is suggested by a color photograph in Lüling (1971), and by a painting in Silverstone (1976, frontisp. II, based on transparency of a paratype, USNM 166904A). The aforesaid painting, however, is printed a little redder than the original transparencies, which are closer to the vermilion of the living frog, as matched in Maerz and Paul's 1930 edition of *A Dictionary of Color* (pl. 2, K12, *fide* Sherbrooke's field notes).

The red hue in Lüling's photograph is close to plate 10, B8, in the *Methuen Handbook of Colour* (Kornerup and Wanscher, 1967). In contrast to this true red, the American Museum specimens collected by Sherbrooke and by the authors were various shades of reddish orange in life, as for example close to plate 7, A8 (AMNH 87925) in the Methuen book. Published photographs of CAS 85151 also show a light reddish orange color, reproduced almost identically from different transparencies (cf., Cochran, 1961, pl. 39; Wenzel and Smith, 1971, p. 6). Three males (AMNH 94803-94805) raised from eggs tended by the male holotype were light orange at maturity, although the holotype itself was a bright red-orange. There seems to be no sexual dichromatism or diel metachromatism, and ontogenetic change is confined mainly to the first month or so of postmetamorphic growth.

TABLE 1
Size and Proportions of Adult[a] *Dendrobates silverstonei*, New Species, in Type Series

Character	N	Mean±1 S.E.	S.D.	C.V. (%)	Range
Snout-vent length (SVL) in mm.[a]	17♂	35.85±0.84	3.47	9.67	28.6-40.0
	6♀	41.83±0.52	1.27	3.03	39.4-42.8
Tibia length/SVL	12♂	0.482±0.003	0.012	2.48	0.46-0.50
	6♀	0.483±0.008	0.019	3.85	0.45-0.50
Head width/SVL	12♂	0.319±0.008	0.026	8.18	0.30-0.36
	6♀	0.308±0.003	0.008	2.44	0.30-0.32
Eye length/tip of snout to eye	12♂	0.854±0.017	0.060	7.08	0.74-0.94
	6♀	0.802±0.023	0.057	7.12	0.70-0.87
Center naris to edge eye/eye length	12♂	0.706±0.022	0.078	10.98	0.60-0.88
	6♀	0.727±0.027	0.065	8.99	0.65-0.83
Width 3rd-finger disc/ finger width below disc	10♂	1.364±0.024	0.076	5.54	1.22-1.44
	5♀	1.418±0.069	0.155	10.93	1.20-1.56

[a]Largest juveniles excluded from table are: AMNH 91846, a subadult male 30.1 mm. SVL, lacking vocal slits. AMNH 91851, a subadult female 32.3 mm. SVL, with small albeit enlarging ova and oviducts.

of fingers varying from gray to nearly immaculate bright orange. Upper third of iris pale bronze with some black suffusion, turning black on lower two-thirds, with minute bronze flecking or not. Bright orange or reddish parts of body turning pale yellowish or grayish in preservative.

Skin of body and hind limbs coarsely granular, especially on back (figs. 1, 6),[1] turning relatively smooth atop head, on forelimbs, and on ventral surfaces. Snout sloping, rounded in lateral profile, truncate to bluntly rounded in dorsal or ventral aspect. Naris situated toward tip of snout and directed posterolaterally; both nares visible from front and from below but not visible from above, although nareal bulges cause the truncated aspect of the snout in dorsal (and ventral) view. Canthus rostralis rounded; loreal region vertical and very slightly concave. Interorbital area wider than upper eyelid. Eye length greater than distance from anterior edge of naris to eye (latter distance 60-88% of eye length); eye/snout length 0.70-0.90 (table 1). Tympanum concealed posterodorsally, where it subcutaneously dips under anterior edge of m. depressor mandibulae; tympanum seen by dissection to be circular or slightly vertically elliptical, with an area greater than 50 percent of eye.

Relative length of *appressed* fingers 3>4≥1≥2, each terminating in slightly expanded disc (fig. 4A); if measured from the base, finger 1 is distinctly longer than fingers 2 and 4, but when appressed their discs overlap and the three are nearly equal. Disc of third finger 1.20-1.56 times wider than distal end of adjacent phalanx, with no appreciable sexual dimorphism (table 1). A large, circular to elliptical tubercle on median base of palm, and a small elliptical one (=inner metacarpal tubercle, but sometimes indistinct) on base of first finger, these tubercles being low, with rounded surfaces; some individuals with suggestion of small, low and poorly defined tubercles on

[1]Granulation is most pronounced on some of the FMNH paratypes, which apparently were killed and preserved by dropping directly into alcohol or formalin; this method seems best for preserving skin texture. The modern procedure of killing frogs in a relaxing agent, followed by positioning and fixation between absorbent, formalin-soaked papers, produces specimens superior for just about every purpose *except* retention of skin texture. Granulation, for example, often is reduced in degree, and skin may turn completely smooth if granulation is weak to begin with.

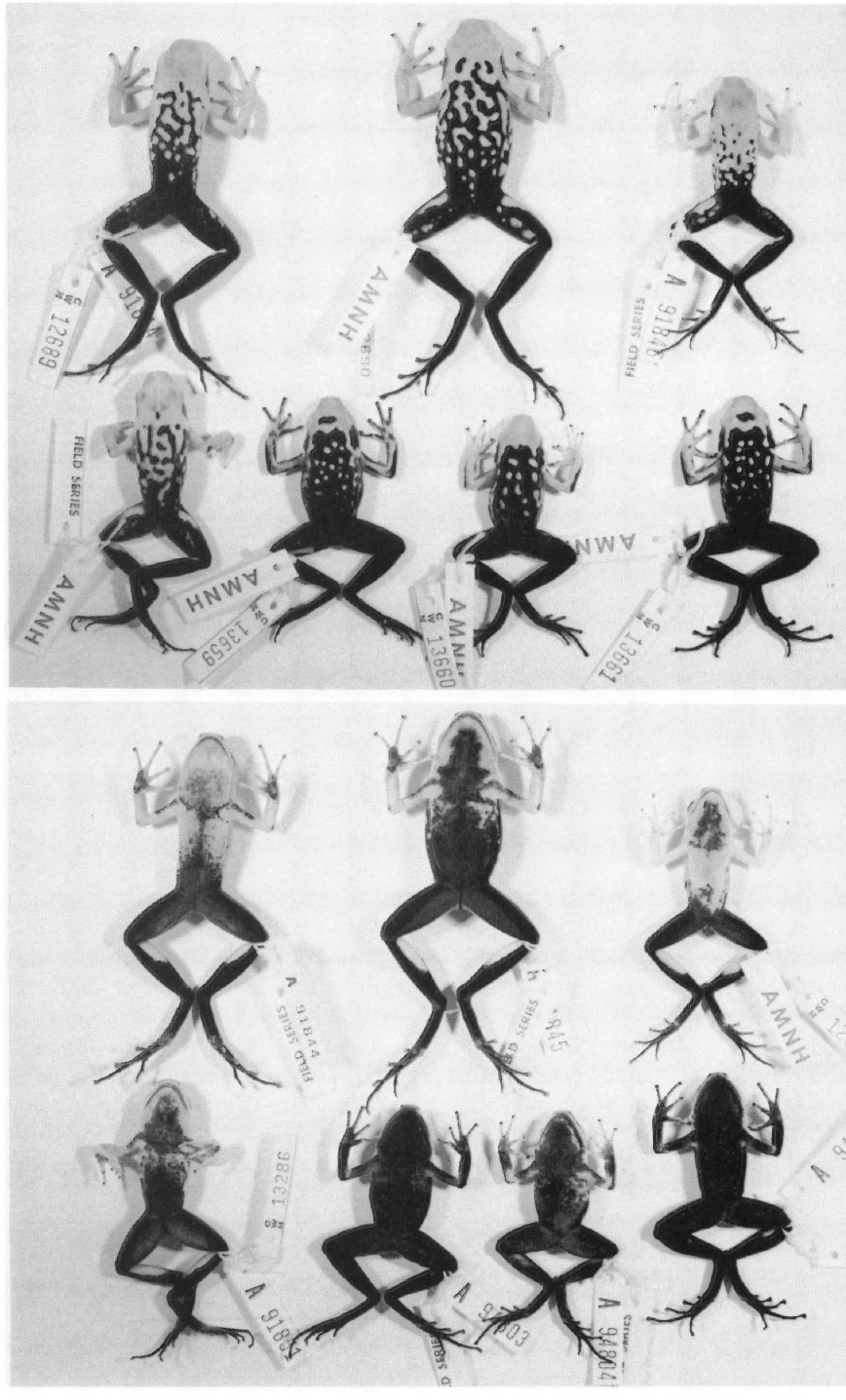

FIG. 2. *Dendrobates silverstonei*, new species. Intrapopulational variation in color pattern of specimens from type locality (1330 m. elev.). Dorsal and ventral views of same specimens: Top rows, left to right, AMNH 91844-91846. Bottom rows, AMNH 91851, 94803-94805.

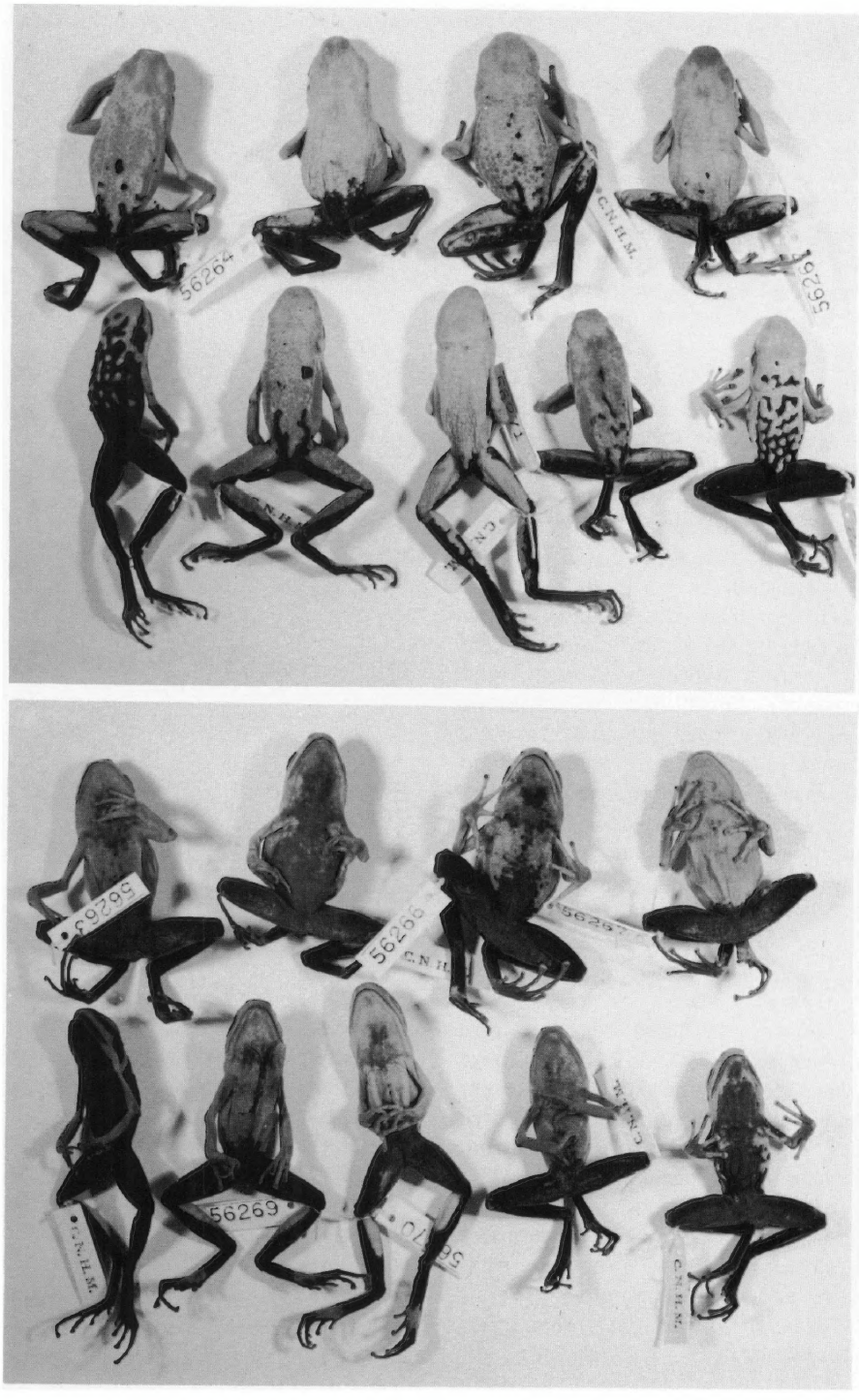

FIG. 3. *Dendrobates silverstonei*, new species. Intrapopulational variation in color pattern of a sample from vicinity of Divisoria (~ 1600 m. elev.). Dorsal and ventral views of same specimens: Top rows, left to right, FMNH 56263-56264, 56266-56267. Bottom rows, FMNH 56268-56272.

palm distad from the large one. One or two subarticular tubercles on fingers (one each on fingers 1 and 2, two each on fingers 3 and 4); subarticular tubercles somewhat protuberant in lateral profile. A few specimens (e.g., FMNH 56268) with a keel-like ridge extending from outer side of large palmar tubercle to proximal subarticular tubercle on finger 4.

Hind limbs moderately long, with heel of appressed limb reaching eye or beyond; tibia/snout-vent length 0.45-0.50 (table 1). Relative lengths of appressed toes 4>3>5>2>1, each terminating in slightly expanded disc (toe discs tending to be slightly wider than finger discs); appressed first toe reaching subarticular tubercle of second. Small inner and outer rounded metatarsal tubercles, and often a smaller or equivalent-sized median metatarsal tubercle in between; some individuals (e.g., AMNH 91845) with suggestion of additional, smaller tubercles distad from aforesaid metatarsal tubercles. One to three subarticular tubercles (one each on toes 1 and 2, two each on toes 3 and 5, three on toe 4). Distal half (or more) of tarsus with a keel-like ridge extending to inner metatarsal tubercle; slightly elevated, oblique proximal end of keel interpreted as tarsal tubercle. Foot tubercles, particularly the subarticular tubercles, protuberant in lateral profile (fig. 4B). Hands and feet lacking webbing, distinct interarticular tubercles, or lateral fringe.

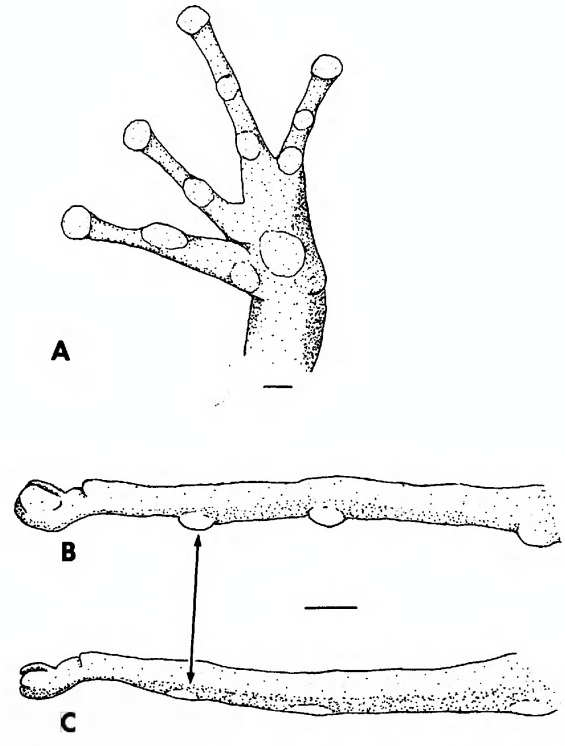

FIG. 4. Palmar view of left hand (A) of *Dendrobates silverstonei*, holotype. Dorsolateral views of left fourth toes of (B) *Dendrobates silverstonei*, holotype, showing relatively prominent subarticular tubercles, and (C) *Phyllobates bicolor*, AMNH 98214, showing low, nonprotuberant tubercles. Lines equal 1 mm.

MYOLOGY AND OSTEOLOGY

MYOLOGY: A few pertinent muscles were examined on AMNH 91847-91849, before these specimens were cleared and stained. The m. depressor mandibulae is comprised of three slips: A large superficial slip originates from the dorsal fascia and conceals a deeper slip originating on the otic ramus of the squamosal bone; a shorter, poorly defined slip originates on the posterior part of the tympanic ring. There is no m. adductor mandibulae externus superficialis. Thus, in the aforesaid characters, the jaw musculature of *Dendrobates silverstonei* is of the normal dendrobatid pattern (Starrett, 1968, p. 100; Silverstone, 1975, p. 4). In dendrobatids generally, the large superficial slip of the depressor mandibulae muscle tends to slightly overlap the tympanic ring and, in any case, holds the skin away from the rear part of the tympanum, thus accounting for the fact that the tympanum is only partially indicated externally.

On the thigh, the deep m. semitendinosus is independent of the superficial m. sartorius, and the distal tendon of the semitendinosus pierces that of the mm. gracilis complex prior to insertion. Noble (1922, pp. 40-41, pl. XV, fig. 6) and Dunlap (1960, p. 9) documented this peculiar condition of the distal thigh tendons in a few species of dendrobatids and other frogs, and Silverstone (*loc. cit.*) found no exceptions in a sample of 41 species of Dendrobatidae.

The flesh of freshly skinned specimens of *Dendrobates silverstonei* was pinkish white,

more like the usual condition in *Colostethus* than the gray or blackish colored flesh of most *Dendrobates* and *Phyllobates*. But melanophores are present, albeit sparse, on blood vessels and muscle fascia at all levels.

OSTEOLOGY: Four cleared and stained paratypic specimens were examined: AMNH 91847-91849 (adult males 32-35 mm. SVL) and FMNH 56265 (about 42 mm. SVL, therefore probably an adult female). The skeleton appears to be relatively plesiomorphic, and the following description is similar to that recently given for *Phyllobates terribilis* (Myers, Daly, and Malkin, 1978).

Skull slightly wider than long. Frontoparietals long, with distinct common suture, and anteriorly distinctly overlapping the sphenethmoid but not fused with it. Sphenethmoid large, extending rostrad partways between nasals. Sphenethmoid with a ventrolateral process extending toward but widely separated from preorbital process of maxillary; palatine bones absent. Nasal bones widely separated from one another, either in narrow posterior contact with sphenethmoid or narrowly separated from it; posterolateral process of nasal wedge-shaped, extending above and slightly past preorbital process of maxillary. Prevomers small, toothless, and widely separated, lying beneath nasals. Maxillary and premaxillary teeth present. Alary processes of premaxillae tipped slightly forward. Maxillary posteriorly shallow, anteriorly with a high facial lobe bearing a small preorbital process. Three specimens with eight presacral vertebrae, none fused either dorsally or ventrally; fourth specimen (AMNH 91848) with nine presacral vertebrae, the last one fused above and below with sacrum. Neural spines of vertebrae not bearing dorsal shields. Ossified omosternum present.

TADPOLES

The male holotype was found on November 2, with a clutch of 30 eggs in a dry leaf (fig. 11). The eggs were kept in a plastic bag for a few days and then transferred to a jar of water; the first tadpoles hatched on November 12, and the last hatched two days later. Five newly hatched larvae preserved on November 13 were in stage 25; the remaining larvae were fed liberally on boiled lettuce. The first individuals metamorphosed on January 18 and the last on February 3. Some loss was incurred, but 19 larvae were preserved in various stages in the period from November 13 to January 24, and one froglet was preserved on March 7. This series (AMNH 94794-94802) is the basis for the following description, which utilizes the staging system of Gosner (1960). Several additional larvae and froglets (USNM 166904B [6 spec.]), in stage 40 and later, were also examined but are excluded from table 2 because of their desiccated condition; Silverstone (1976, pp. 5, 7, 21) provided basic data from this series.

HABITUS AND PROPORTIONS: The head and body are depressed (width > depth), slightly convex above and flattened below. Eyes and nostrils are directed dorsolaterally from a dorsal position. The spiracle is sinistral and the anus dextral (median by stage 42). Head-body length, from hatching through stage 44, changes from about 4.4 to 12.5 mm. (table 2). Total length changes from a minimum of about 12 mm. to a maximum of about 30 mm. (~ stage 40), and then decreases due to tail resorption.

Tail length comprises 58-65 percent of total length through stage 42 and then drops markedly (45% in a stage-43 larva). The greatest depth (from upper edge dorsal fin to lower edge ventral fin) of the low-finned tail averages only 16.2 percent (16-17%, $N = 5$) of total length in stage-25 hatchlings, but soon thereafter it increases to an average of 20.3 percent (18-22%, $N = 12$) in stages 26-42.

PIGMENTATION: In life, the tadpoles are grayish or blackish brown, with vague darker spotting (well shown in photograph in Wenzel and Smith, 1971). In preservative, the tadpoles are light brown over the head and body, turning pale brown on the throat and also sparsely pigmented with brown on the belly (which in hatchlings is yolk-yellow); some larvae have a few small, irregularly placed spots of slightly darker brown. Stage-25 larvae have a speckling of brown over most of the tail, except on the ventral fin; in subsequent stages, the caudal pigment is concentrated to form a weak pattern

TABLE 2
Measurements (in Millimeters) of *Dendrobates silverstonei* Larvae[a]

Stage	Day	N	Head-Body Length	Total Length	Greatest Tail Depth
25	1	5	4.3-4.7 ($\bar{X}$ = 4.52)	11.9-13.0 ($\bar{X}$ = 12.42)	1.9-2.1 ($\bar{X}$ = 2.02)
26	18	3	6.4-6.8 ($\bar{X}$ = 6.60)	15.6-17.0 ($\bar{X}$ = 16.10)	3.5-3.7 ($\bar{X}$ = 3.57)
28	26	3	8.0-8.5 ($\bar{X}$ = 8.33)	20.7-21.6 ($\bar{X}$ = 21.07)	4.1-4.6 ($\bar{X}$ = 4.30)
31	38	1	10.0	27.0	5.4
32	38	1	9.5	25.7	4.5
37	52	1	11.5	29.5	5.4
37/38	52	1	11.5	30.5	5.4
41	62	1	11.6	29.6	6.4
42	62	1	11.6	28.6	6.0
43	67	1	12.2	22.3	3.0
44	73	1	12.4	_[b]	_[b]

[a]Laboratory reared.
[b]Tail damaged.

of light brown blotches, except that the ventral fin remains mostly clear. There tends to be a scattering of minute white flecks (probably silver or bronze in life) over the entire tadpole, especially conspicuous on the tail fins.

There is little ontogenetic change in pigmentation until after stage 42, when the forelimbs have appeared: Sometime before metamorphosis, living four-legged larvae were noted to have turned dull yellow-gold on the forelimbs, snout, and upper eyelids, with the body being dark brown (but see Postmetamorphic Changes following).

MOUTH PARTS: The mouth is directed ventrally in stage-25 hatchlings and directed more anteroventrally in later stages, but the change is slight (and conceivably due to preservational effects). The tooth-row formula is 2/3, with the second upper row being broadly broken above the beak (fig. 5). Stage-25 hatchlings have a superficial appearance of having only 1/2 tooth rows, since the denticles of the second upper and third lower rows are not yet keratinized. The beak is shallowly keratinized (i.e., not appearing massive), with very finely toothed cutting edges; the lower beak is broadly V-shaped. The oral disc is laterally indented. The anterior edge of the oral disc is nude, but its lateral and posterior edges bear a single (in all stages) row of *pointed* papillae.

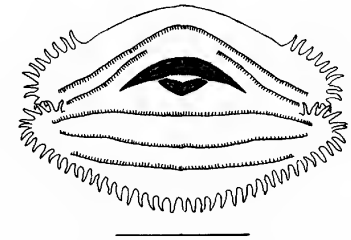

FIG. 5. Mouth of *Dendrobates silverstonei* tadpole, stage 28 (semidiagrammatic, based on AMNH 94796). Line equals 1 mm.

POSTMETAMORPHIC CHANGES

As mentioned above, late tadpoles acquired dull yellow pigmentation on forelimbs, snout, and upper eyelids. The dark brown of the larval body darkened to black in the froglets and the yellow changed to light orange. The orange area expanded over the head, and some orange spots appeared on the dorsum. This pattern was essentially developed within a month or so and was little changed at an age of 5 months (fig. 6, left). Little further expansion of the orange areas had occurred by 12 months of age (fig. 6, right). Three laboratory-reared males (AMNH 94803-94805) are believed to have attained sexual maturity (judged by opened vocal slits) by at least age 12-14 months, although when pre-

served they were somewhat smaller (28.6-31.5 mm. SVL) than the smallest wild-caught male adult (32.5 mm.). It also is to be noted that the light orange color of these frogs never changed to the reddish orange of wild-caught individuals from the same locality (p. 4n), although samples are too small to suggest an explanation for the differences.

The preceding description of color-pattern ontogeny pertains to the type locality. In a population closer to Divisoria, according to Lüling (1971, pp. 170-172, figs. 5-6), the light pigmentation does not appear until several days *after* metamorphosis, but with the adult coloration being similarly attained in a month or so. If the difference is actually a reflection of interpopulational variation, it would seem that frogs having the least amount of bright color as

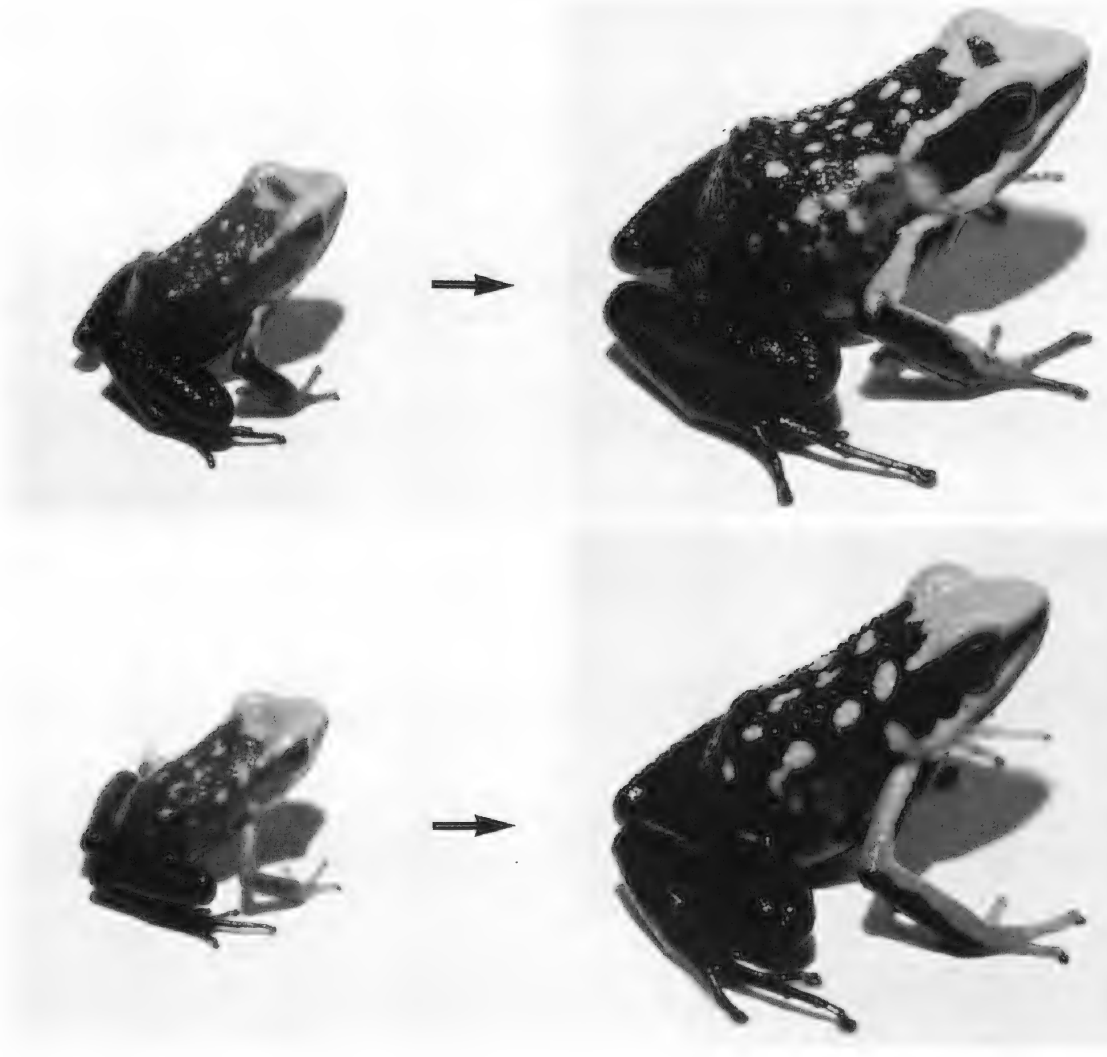

FIG. 6. Postmetamorphic growth from 5 to 12 months of age in two *Dendrobates silverstonei*. Both frogs laboratory-reared from eggs found with the holotype (see fig. 11), approximately ×1.9. Ontogenetic changes in color pattern were slight during the 7-month interval.

Top: AMNH 94803. *Bottom*: AMNH 94804. Both individuals are males that were judged to be sexually mature (i.e., with open vocal slits) when preserved 45 days after taking photographs on right (see also fig. 2, middle two specimens in bottom row).

adults (fig. 2) may start acquiring that pigmentation somewhat earlier than frogs which finish brighter (fig. 3).

There is no indication of stripes during development of the color pattern, in contrast to the situation in *Phyllobates* (fig. 3 in Myers, Daly, and Malkin, 1978).

SKIN ALKALOIDS AND TOXICITY

Four paratopotypes, all adult males (AMNH 91847-91850), were skinned after capture in early November 1974.[1] The four skins, which had a combined weight of 2.0 g., were extracted in methanol, and the alkaloid fraction was later analyzed by thin-layer chromatography (fig. 7) and combined gas chromatography-mass spectrometry (fig. 8). Methodology is given in Myers and Daly (1976a) and Daly et al. (1978).

Five alkaloids were detected; none is novel, each compound having been previously isolated from other species of the genus. The alkaloids of *Dendrobates silverstonei* are distributed according to the classification of Daly et al. (1978) as follows:

PTX-C CLASS	PTX-A CLASS	UNCLASSIFIED
205*[a]	**251D***	**265**
	307C	
	323B*	

[a]Major compounds are designated by an asterisk (Daly et al., 1978, table 1).

Since only a few of the dendrobatid alkaloids have been individually named, the compounds are designated by their molecular weight in boldface type; an added letter, if present, codes the compound from others of identical weight. Empirical formulae, fragmentation patterns, and other data are given in Daly et al. (1978).

[1]A skin of another paratype (AMNH 87924, from Divisoria) that had been carried alive to New York by Wade C. Sherbrooke, was examined in 1971 by thin-layer chromatography and mass spectrometry. Results were comparable to the present analysis except in being less complete, since the sensitive technique of gas chromatography had not yet been successively applied to the study of dendrobatid alkaloids. This and other analytical techniques, their strengths and their limitations, are discussed in Myers and Daly (1976a).

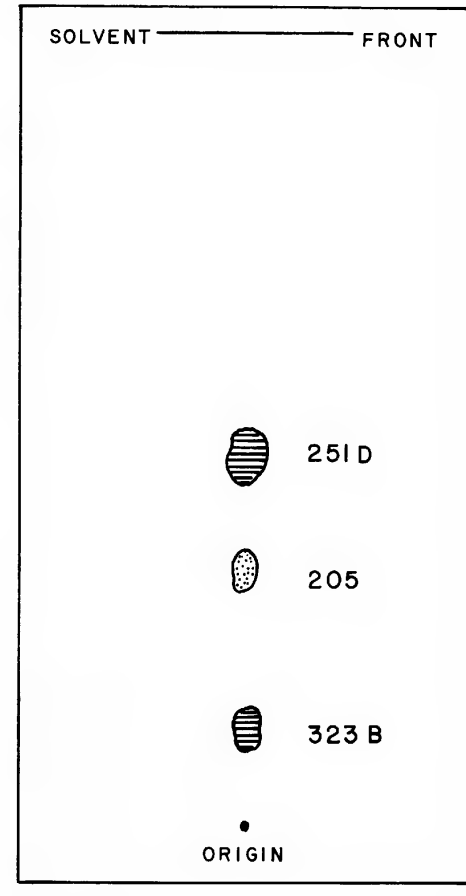

FIG. 7. Representation of thin-layer chromatoplate of alkaloids from a population sample of *Dendrobates silverstonei* (four paratopotypes, November, 1974). A sample of 10 μl of methanolic alkaloids equivalent to amount in 10 mg. wet skin was applied at the origin.

Designations are based on the known or suspected (*re* **205**) R_f values of compounds identified in the unresolved alkaloid fraction by combined gas chromatography-mass spectrometry (fig. 8). Spot intensities are depicted as follows: Horizontal pattern=moderate amounts; dots=small amounts (reference standards are figs. 1-2 in Myers and Daly, 1976a).

Alkaloid **205**, with a base peak at m/e 138, is probably a member of the pumiliotoxin-C class, although many assignments to this class of decahydroquinolines are considered tentative. Of the three pumiliotoxin-A class alkaloids, compound **323B** (allopumiliotoxin B) has elsewhere been found in isolation from

pumiliotoxin B (= **323A**, not detected in *silverstonei*) only in the Ecuadorian *Dendrobates tricolor* (study in progress). One trace alkaloid (**265**), detected as a minor constituent in various *Dendrobates*, remains unclassified because of its atypical mass spectrum and a suspicion that it might actually be a degradation artifact of some other compound (Daly et al., 1978, pp. 172, 185).

Thus, the skin toxins of *Dendrobates silverstonei* consist primarily of alkaloids of the pumiliotoxin-A class. Although pumiliotoxin-A compounds tend to be more toxic than those in the other four classes of dendrobatid piperidine alkaloids, the secretions of *D. silverstonei* are not especially toxic: An extract of the unresolved alkaloid fraction, equivalent to the amount of alkaloids in 100 mg. wet skin (1 skin ~ 500 mg.), was injected subcutaneously into a 20-gram white mouse (NIH general purpose type). The mouse then exhibited severe locomotor difficulties, partial paralysis of the hind limbs, wobbling gait, gagging, labored breathing, and occasional mild convulsions, but recovery occurred after three hours. Similar injections of extracts from some populations of *Dendrobates auratus* and *D. pumilio* may cause death in as little as 6 minutes. The lesser toxicity of *D. silverstonei* is due in part to the unexpected absence (see above) of the widespread and highly toxic pumiliotoxin B, and in part to the small amounts of alkaloids actually present in the skin. The area under the gas chromatographic peaks is indicative of the amount of alkaloids present. Compared with species for which alkaloids have been quantified (compare fig. 8 with Myers and Daly, 1976b, pp. 9-10), *Dendrobates silverstonei* would appear to possess less than 50 μg of alkaloids per 100 mg. of skin.

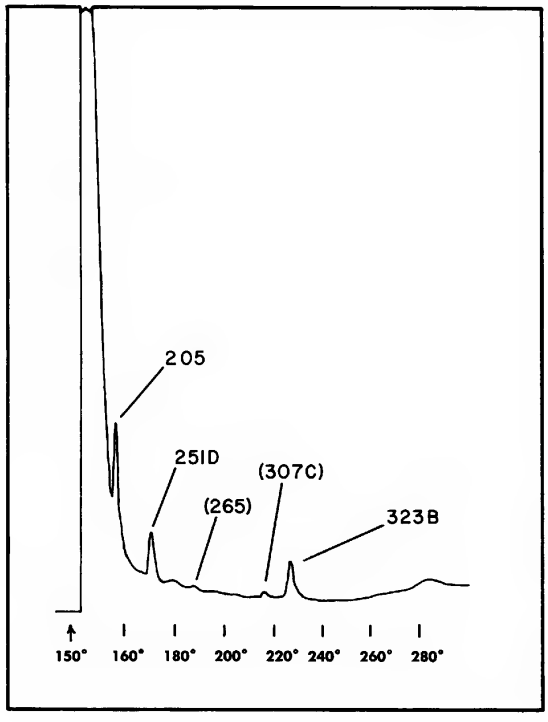

FIG. 8. Gas chromatogram of alkaloids from a population sample of *Dendrobates silverstonei* (four paratopotypes, November, 1974). Chromatography was run with 2 μl of methanolic extract containing concentrated alkaloids equivalent to amount in 2 mg. of wet skin.

Alkaloids are designated by their molecular weights; parentheses indicate trace compounds. The corresponding protonated molecular ions of these alkaloids were identified in separate computer-assisted analysis by combined gas chromatography-mass spectrometry.

The slight toxicity of the alkaloid fraction indicates that the steroidal batrachotoxins are *not* present in *Dendrobates silverstonei*, since the minimal lethal dose of (homo)batrachotoxin is only about 0.05 μg in a 20-gram mouse. An independent chemical assay of comparable sensitivity was conducted with the reagent 4-dimethylaminocinnamaldehyde following chromatography of an amount of alkaloid fraction equivalent to 100 mg. of wet skin; methodology was the same as detailed in Myers, Daly, and Malkin (1978, p. 337) except that the present sample size is tenfold larger (100 mg. equivalent vs. 10 mg.). There was no indication of batrachotoxin or homobatrachotoxin by this test either, and these extraordinarily potent poisons must be assumed absent in *Dendrobates silverstonei*. More will be made of this in the discussion of relationships.

DISTRIBUTION, GEOGRAPHIC VARIATION, AND NATURAL HISTORY

DISTRIBUTION AND VARIATION: *Dendrobates silverstonei* may be confined to the Cordillera Azul, which starts from a northeasterly spur of

the Andes at about 9° 20′ south latitude and then stretches for a few hundred kilometers northwestward, parallel to the main axis of the higher Andes and separated from them by the valley of the Río Huallaga. The Cordillera Azul lies mostly below 2000 meters elevation, and presumably it is blanketed by wet montane forest over most of its length (fig. 9). This frog thus would seem to have a potentially long albeit narrow range, although it presently is known only from 1330 to some 1600 meters of elevation in the vicinity of Divisoria, at about 9° south latitude.

Despite the small area from which samples have been taken, some geographic variation in color pattern is evident, as is readily visualized by comparison of figures 2 and 3. Specimens from the type locality at 1330 meters elevation have extensively black-marked bodies, whereas most individuals from Divisoria (~ 1600 m.) have very little black pigmentation on their bodies. Also, there may be an interpopulational difference in the ontogenetic development of the color pattern (see Postmetamorphic Changes). In addition, the few data on color in life (see p. 4n) suggest that the bright body coloration may vary from mostly reddish orange or orange in some populations (e.g., at type locality), to mainly red in others.

Such microgeographic variation is not at all uncommon in *Dendrobates* and may in fact be the rule rather than the exception. Because of this, it will not be surprising if *D. silverstonei* specimens from some distant part of the Cordillera Azul prove manifestly different from those in the type series.

HABITAT: *Dendrobates silverstonei* occurs in wet montane forest that is clearly evergreen, although subject to seasonal fluctuation in rainfall. At the type locality (1330 m. elev.), this forest grows over moderate to steeply sloped terrain, on dark brown soil [red-brown in some nearby areas]; drainage is by rocky, clearwater streams. Where uncut, the forest is comprised mainly of straight-boled trees of moderate height; there is a scattering of large, buttressed trees and tall stilt-root palms. The lower vegetation is mainly treelets, or saplings, and small palms, with a few tree ferns. The moss layer on tree trunks is thin and often patchy; bromeliads are common and sometimes grow on the ground, although not in dense populations. Lianas trailing from the trees are common but were not noted to occur in dense tangles. In general, little machete work was needed to pass through this forest.[1] At ground level, vegetation is sparse, with more ferns than herbaceous plants. Leaf litter is thin and becomes rather dry after several rainless days, as was the situation when we first worked at the site on November 2 and 3; a long, steady rain occurred during the night and early morning of November 4-5.

We did not collect *Dendrobates silverstonei* in the undisturbed forest described above, but obtained our specimens in and around brush piles in an adjacent cut-over area (fig. 9, bottom). Lüling (1971) also stressed that he found these frogs in open places in the forest and in cleared areas near a tea plantation. Although forest frogs generally are simply much easier to find in newly and partially cleared areas than in undisturbed forest, some dendrobatids actually do seem to concentrate and flourish in such edge situations. For example, the widely distributed *Dendrobates trivittatus* may be found in deep rain forest, but it nonetheless is also drawn to some edge situations. For example, based on vocalizations, *D. trivittatus* was found to be nonrandomly concentrated in piles of logs and brush along a half-year-old survey road through virgin forest in Surinam; the frogs must also have occurred in adjacent, undisturbed parts of the forest, but none was heard calling there.[2] *Dendrobates trivittatus* is chosen as this example for the reason that it is suggestively close to *D. silverstonei* in size and general habits and has a very similar call. But even so, our experience with *D. silverstonei* is too lim-

[1]But at higher elevations we encountered some nearly impenetrable growths of a moderate-sized bamboo in the forest understory, possibly indicating disturbance. The forest is of course becoming increasingly disturbed near the gravel highway, and some areas have been completely cleared for extensive tea plantations.

[2]Observations made August 15-18, 1975, by C. W. Myers and his son Charles, in company with M. S. Hoogmoed and W. N. Polder, near "Suralco Camp V," headwaters Djoeka Creek, 620 m., central Lely Mountains, Marowijne District, Surinam. For arranging this trip, a debt of gratitude is owed Dr. Hoogmoed, Rijksmuseum van Natuurlijke Historie, Leiden.

FIG. 9. Habitat of *Dendrobates silverstonei*. *Top*: View of the Cordillera Azul, looking south from 1600 m. elev. on Tingo María-Pucallpa Road, between Divisoria and Boquerón del Padre Abad. *Bottom*: Cut-over forest at the type locality, 1330 m. elev., where the frogs were found mainly in piles of logs and brush. (Both photographs, November 5, 1974.)

ited to draw firm conclusions regarding its microhabitat preferences.

So far as known, *Dendrobates silverstonei* is the only toxic dendrobatid that occurs in this montane forest, although a presumably nontoxic species is present (*Colostethus* sp., AMNH 86501, 86502, from Divisoria). *Dendrobates pictus*, *D. quinquevittatus*, and *D. trivittatus* occur at lower elevations along the Tingo María-Pucallpa road. Because of its similar size and habits, only *trivittatus* would seem capable of providing significant competition for *silverstonei*, but it is unlikely that their habitats overlap to any great extent, if at all. The highest that we found *Dendrobates trivittatus* was 720 meters in the Huallaga drainage (14 km. air line NNE Tingo María), and, based on a survey of numerous museum specimens of the species, Silverstone (1976, p. 47) reported an elevational range of 20-680 meters above sea level. The elevational gap in the Cerro Azul region is about 600 meters between our uppermost station for *D. trivittatus* (720 m.) and the lowermost one for *D. silverstonei* (1330 m.).

ACTIVITY: *Dendrobates silverstonei* is a diurnal, terrestrial frog. The ones that we found were all on the ground, and Lüling (1971, p. 169) saw little climbing by captives in a roomy terrarium. Lüling (*loc. cit.*) observed aggressive head jerking, pushing and biting by his captives; various kinds of aggressive behavior are widespread among dendrobatids, but the biting behavior seems unusual and needs to be confirmed. Because these frogs are brightly colored and active by day, the same author implied that they are not shy, but, compared with many dendrobatids, they really are timid and quite wary. Their alertness is shared by *D. trivittatus*; both species tend to be hard to approach and usually are quick to hide, especially in piles of logs and brush if available. But, at the type locality, *D. silverstonei* also called while hidden within such places on the ground, whereas *trivittatus* often (but not always) calls while perched on logs or in low vegetation.

We heard only an occasional call at the type locality on November 2 and 3, but activity was much greater on November 5, when the forest was wet from a long rain (see Habitat above) and several frogs were calling frequently from concealed places. But there seemed to be little or no activity before late morning. We searched intensely starting at 10 A.M., but neither saw nor heard anything until 11 A.M., when calling suddenly commenced and two frogs were found moving about. If that pattern of activity is typical, it is an interesting contrast to the lowland *Dendrobates trivittatus*, which throughout its range tends to call mainly in early morning and late afternoon, with calling being less frequent during the middle of the day. On our way up to the type locality on November 5, we found *D. trivittatus* still calling at 9 A.M. (14 km. NNE Tingo María, 720 m.), whereas *D. silverstonei* only commenced calling higher in the mountains two hours later. Although we do not know the extent to which such times of activity might be modified by local weather conditions or seasonal climatic change, it did seem evident that total activity of *D. silverstonei* had been suppressed during a brief dry spell, and increased after a good rain.

VOCALIZATION: The call of *Dendrobates silverstonei* (fig. 10B) is a train of uniform notes that are heard as short (~ 0.08 sec.), *abrupt* whistles, which are distinctly spaced (~ 0.1 sec.), being emitted at a rate of about 4-6 notes per second. Call length is 20-27 seconds ($\bar{X}$ = 24.4 sec.) in 14 recorded calls from two individuals; one additional call is only 11 seconds long. The call sometimes starts or ends a little slower than at midcall, and spacing between calls is quite irregular, varying from one or two seconds to hours. The dominant frequency is held rather constant throughout the call at about 2400 or 2500 Hertz.[1]

In some dendrobatids, note repetition rate is positively correlated with temperature, and note

[1]A fundamental frequency at 1200-1250 Hz, and from one to five higher harmonics (above the dominant) may be present on the sound spectrogram *or absent*, depending apparently on modulation control and perhaps microphone distance during original recording, and/or on machine-adjustment variables during production of the spectrogram. Because of such variability, we discount harmonic structure as being taxonomically useful, at least for present analysis of dendrobatid calls. There are many ways of distorting sound and sound spectrograms, and we fear that machine-induced artifacts may be commonplace to published spectrograms.

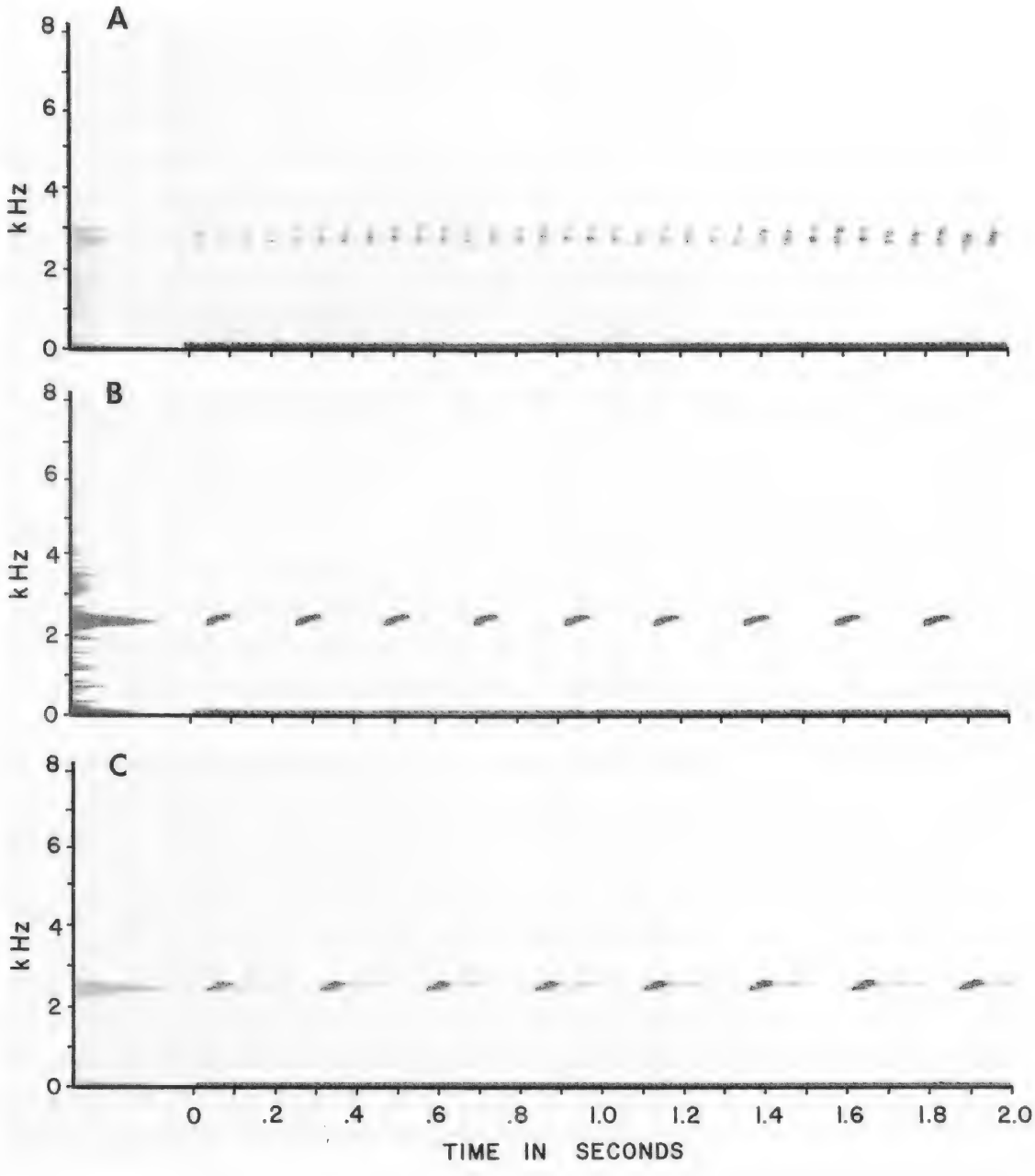

FIG. 10 A-C. A trill call (A) and two retarded trill calls (B-C) of South American *Dendrobates* spp. Narrow-band sound spectrograms, 45-Hz filter, made from field recordings. A. *Dendrobates leucomelas*. Portion of 9-second-long trill call from La Escalera, 500 m., about 100 km. [by road] S Río Cuyuni, Estado Bolívar, Venezuela. Recorded at 10:40 A.M. on June 10, 1968, by Paul Schwartz, using parabolic reflector; temperature not recorded. Section is of fifteenth note from left. (Neotropical Inst. no. 36; copy on AMNH reel 211.) B. *Dendrobates silverstonei*, new species. Portion of 26-second-long retarded trill call from type locality in Cordillera Azul, 1330 m., Dept. Huánuco, Peru. Hidden individual calling at midday within brush pile, where air temperature was 18.5° C., November 5, 1974. Section is of first note on left. (AMNH reel 179.) C. *Dendrobates trivittatus*. Portion of 39-second-long retarded trill call of AMNH 90916, from headwaters Djoeka Creek, 620 m. in central Lely Mountains, Marowijne District, Surinam. Recorded 8 A.M. at air temperature of 20.8° C., August 19, 1975. Section is of third note from left. (AMNH reel 181.)

duration is negatively correlated (Myers and Daly, 1976a, pp. 231-233). At least the note repetition rate may be similarly influenced in *Dendrobates silverstonei*, but data are scant and the possibility of significant individual variability cannot be excluded.

VARIATION IN NOTE REPETITION RATE[a]

Temperature	N	Notes per Second Mean	Range
18.5° C.	6[b]	4.80	4.5-5.0
23.0° C.	9[c]	5.78	5.0-6.0

[a]Determined from 2.0-second intervals on sound spectrograms, from middles of 15 calls.

[b]Calls from one frog, seemingly not interacting with others, recorded November 5, 1974, at type locality.

[c]Calls from one paratypic frog (AMNH 87925) isolated in terrarium at AMNH, recorded January 4, 1972.

Recordings have thus far been obtained from about half the species of the *Dendrobates-Phyllobates* complex. A portion of these calls have been described and grouped into several call-types, onomatopoetically named *buzz calls, chirp calls*, and *trill calls* (Myers and Daly, 1976a; Myers, Daly, and Malkin, 1978). We are continuing this analysis and here establish *retarded trill calls* as a fourth class of dendrobatid vocalizations, to include the calls of *Dendrobates silverstonei* and *D. trivittatus*. A retarded trill call is a train (often long) of uniform, short, and relatively musical notes that are emitted at a speed of less than 10 per second. Although the individual notes in this kind of call may be longer and more narrowly tuned than in some trill calls (see fig. 10), the real difference is in the slower rate at which the notes are emitted in the retarded call. The call of *Dendrobates silverstonei* becomes a definite trill when a recording is played at twice normal speed. It is too early to attempt a phylogenetic analysis, and some other classes of calls remain to be described, but the four call-types so far defined are distributed as follows: (1) All *Phyllobates* (*sensu stricto*) and some *Dendrobates* have trill calls, both plesiomorphic and apomorphic species being included in the latter. (2) Retarded trill calls are documented only for a few plesiomorphic species of *Dendrobates*. (3) Chirp calls are known only for highly apomorphic *Dendrobates* of the *pumilio* and *histrionicus* groups (excluding *D. leucomelas* from the latter group). (4) Buzz calls, originally based on few species, have been subsequently found to characterize a diversity of plesiomorphic and apomorphic *Dendrobates*, including most (but not all) species currently assigned to the *minutus* group. As we have previously noted (1976a, p. 238), there appears to be some correlation between type of call and life-style, although phylogenetic correlation is not always evident. Whether *Dendrobates silverstonei* and *D. trivittatus* are closely related or not, both give nearly identical calls that, although loud and long, are quite difficult to locate by at least some potential predators (ourselves), and both frogs are wary and quick to hide. The retarded trill call might be both conspicuous to conspecifics and difficult to locate by predators, and thus suitable to the life-style of a social but vigilant frog.

REPRODUCTION AND LIFE HISTORY: Courtship has not been observed, unless confused with aggressive behavior (see Activity). Since *Dendrobates silverstonei* is a relatively plesiomorphic species, it would not be surprising to find that mating amplexus has been retained (see Myers, Daly, and Malkin, 1978, p. 324). Lüling (1971, p. 168) speculated that there is more than one laying period. Because the species occupies humid evergreen forest in which the dry season is not severe, we would predict that individual females lay repeatedly throughout all or most of the year.[1]

On November 2, 1974, a clutch of 30 eggs was found on a curled dry leaf that was overlain and completely concealed by another leaf on the cut-over forest floor. The eggs were closely packed in a single layer and obviously represented a single clutch. They were attended by a male frog (the holotype), which kept his

[1]A single captive female of another species (*Dendrobates tricolor*) has, at the time of this writing, averaged 2.5 clutches monthly over a period of 21 months.

position even when the leaf with eggs was placed in a plastic bag and later removed for photographing (fig. 11). The adult frog did not move to defend the eggs but remained crouched at the edge of the clutch. There was no calling activity from this or neighboring males when the eggs were found (late afternoon of a dry day), but a male *Dendrobates trivittatus* was found calling while overlooking a single clutch of 34 eggs, in a similar forest-floor situation in Surinam (AMNH 87679, Raleigh Cataracts, 50 m., Coppename River).

The *Dendrobates silverstonei* eggs were placed in water after a few days and commenced to hatch 10 days after being found (see Tadpoles); larvae metamorphosed and left the water 67-83 days after onset of the 3-day hatching period, and the froglets started feeding on *Drosophila* about 4 days after leaving the water. A few frogs raised in captivity seemed to take at least a year to reach sexual maturity (fig. 6).

It seems that at least half (if not all) of the tadpoles must be carried to water in one trip, judging from the sizable numbers of larvae found on the backs of two male nurse frogs: (1) Edward S. Ross found one (CAS 85151) on September 29, 1954; the larvae were not saved, but, from comparison of two photographs of this specimen (fig. 12; Cochran, 1961, pl. 39), we estimate that it was carrying 17 or more larvae. (2) On October 8, 1966, Wade C. Sherbrooke found a male carrying tadpoles roughly estimated as 15 in number, of which some were lost according to his field notes for WCS 2540 [= USNM 166904A,B—based on the number actually preserved, Silverstone (1976, p. 21) thought that the frog was found with only six tadpoles]. The preceding carriers were found in September and October, whereas our specimen

FIG. 11. Male nurse frog with terrestrial clutch of 30 eggs, approximately ×1.8. This specimen (see also fig. 1) is now the holotype of *Dendrobates silverstonei*, new species. Two frogs reared from these eggs are shown in figure 6.

FIG. 12. Male nurse frog carrying tadpoles, approximately ×2.5. Photograph of a paratype (CAS 85151) of *Dendrobates silverstonei*, courtesy of Edward S. Ross.

probably would have transported its tadpoles in mid-November, and Lüling (1971, p. 167)[1] mentioned carriers that were found in June. We suspect that the activity occurs yearlong.

Since the larvae can hatch and appear to develop normally if the terrestrial eggs are artificially placed in water, tadpole carrying evidently serves only the mechanical function of moving tadpoles from the nest to water. There is no factual basis for Cochran's (1961, pl. 39 caption) statement that the larvae of this species undergo development on their father's back; her account (p. 107) of the life history of *Dendrobates* is fictional. Lüling (1971) found tadpoles of *Dendrobates silverstonei* in water-filled ruts made by bulldozers, and provided a chemical analysis of the water. Ross found his nurse frog in a roadside ditch fed by spring seepage (Alan E. Leviton, *in litt.*). This habit of depositing tadpoles in ground water (vs. in water-containing plants or tree holes), and also such a relatively large number of eggs (~ 30 vs. only 2-3 in some species), are interpreted as plesiomorphic traits within the genus *Dendrobates* (*sensu lato*).

PREDATION: *Dendrobates silverstonei* seems to produce relatively small amounts of skin alkaloids and is not as toxic as species of *Phyllobates* and many other *Dendrobates* (see p. 13). But, as would be expected from its conspicuous and presumably aposematic coloration, the toxins produced are sufficient to deter some predators. Lüling (1971, p. 172) offered a specimen to a frog-eating snake, which had been caught in the frog's habitat. The frog was seized and immediately released, whereupon the snake shook its head and attempted to rub its mouth against branches, while gaping the

[1]Lüling's (*loc. cit.*) secondhand description of a honeycomb impression (*Waben*) on the nurse frog's back was based on erroneous observation of the tadpoles themselves, as corrected in a note appended to the end of his paper (p. 174). Similarly, Silverstone's (1976, pp. 27-28) secondhand account of *Dendrobates anthonyi* tadpoles being contained in a fluid-filled "blister" is also most certainly based on faulty observation of a densely packed mass of glistening tadpoles; we have confirmed normal tadpole carrying in this species.

mouth for 6 minutes; the snake recovered soon thereafter. Lüling identified this snake as a *Chironius*, and it seems likely to be the same species as the one snake that we found at the type locality of *D. silverstonei*; our specimen (AMNH 113017, *Chironius* sp.) contained only the remains of a nondendrobatid frog.

Owing to the large spectrum of potential frog predators in humid tropical forest, the problem of predation on toxic dendrobatids is not easy to address, but observations such as the above should not be taken to mean that the frogs are completely immune from predation. The wary behavior of *Dendrobates silverstonei* suggests otherwise, however conspicuous its warning coloration might be. A species of snake (*Leimadophis epinephelus*) occurring in Central America and northwestern South America is tolerant of a variety of anuran skin secretions, including toxins of both *Dendrobates* and *Phyllobates* (Myers, Daly, and Malkin, 1978, p. 327), and other potential predators of these frogs doubtless occur.

SYSTEMATICS

Cochran (1961) and Cochran and Goin (1970) confused this species with *Phyllobates bicolor*, probably because of similar body length and the somewhat similar color patterns of preserved specimens (pale body, dark on hind limbs). Such confusion is possible because of the considerable morphological similarity among many species of dendrobatids. Still, specific differences are detectable from preserved specimens alone, and there seems little chance that the two species would be confused in life. The Colombian *Phyllobates bicolor* (fig. 13) differs from *Dendrobates silverstonei* in being more robustly built for its length, in having much smoother dorsal skin, in having a less truncate snout, in having a shorter tarsal keel, and in having low, nonprotuberant tubercles on hands and feet (cf., figs. 4B, 4C). In life, the smooth, yellow or orange dorsum of *P. bicolor* has a golden sheen that gives it a much different appearance. The coloring of the limbs, although variable, also is different from *D. silverstonei*, which has the hind limbs either mostly black or else blotched with the same color as on the body, sometimes including a concealed calf spot; in known populations of *P. bicolor*, all four limbs are either black, with blue or gold speckling, or else suffused with a light greenish or yellowish wash that is of different hue from the body (as in fig. 13), and there is no calf spot. *Phyllobates bicolor* also differs notably in having a trill call and in being less timid and not so quick to seek cover when being approached. Because of differences in skin chemistry, an individual *P. bicolor* is hundreds of times more toxic than *D. silverstonei*.

Silverstone (1976, pp. 7, 20) recognized that the new species is distinct and, under the name "*Phyllobates* species," he doubtfully placed it in the *P. bicolor* group because of its superficial resemblance to *bicolor*. But many of the above differences between *bicolor* and *silverstonei* also apply to comparisons between *silverstonei* and other members of the *bicolor* group, and we are unable to support the notion of common generic status. The species *bicolor* is the nomenclatural type of the genus *Phyllobates*, which was recently redefined on the basis of a novel synapomorphy, namely the batrachotoxin class of steroidal skin alkaloids (Myers, Daly, and Malkin, 1978). No batrachotoxin alkaloids were detected in the skin secretions of *Dendrobates silverstonei*, although the assay techniques should have revealed the existence of as little as 0.05 μg per 100 mg. of skin (i.e., $\sim$ 0.25 μg/frog).

If overall phenetic similarity were really great, one might perhaps hypothesize that *silverstonei* and members of the *bicolor* group actually do form a monophyletic group, with batrachotoxins having been either lost in *silverstonei* or else occurring in presently undetectable trace amounts. But such a hypothesis could be corroborated only by other synapomorphies, which we fail to find. The color pattern of *silverstonei*, which is the main reason for prior confusion, seems to be an autapomorphy that presently provides no clue to relationships. The dorsal black markings and the concealed calf spot of some individuals have no parallel in *Phyllobates*. Furthermore, *silverstonei* lacks a metallic sheen to its bright color, and there is no indication of dorsolateral

FIG. 13. *Phyllobates bicolor* (AMNH 98209) from upper Río San Juan, 500-600 m., Dept. Risaralda, NW Colombia. This specimen had a golden orange body and pale green limbs, which in some populations are black (cf. fig. 8C in Myers, Daly, and Malkin, 1978). Approximately ×1.3.

stripes in the ontogenetic development of its color pattern.[1] Thus, resemblances between color patterns are actually rather slight and most likely due to convergence.

The presence of piperidine-based alkaloids in the skin of *silverstonei* confirms that the species belongs to the monophyletic group consisting of the presently recognized genera *Dendrobates* and *Phyllobates*. Since we exclude it from the latter, *silverstonei* automatically belongs to *Dendrobates* (*sensu* Myers, Daly, and Malkin, 1978, pp. 332-333). It is not our purpose to discuss internal relationships of *Dendrobates* at this time, but similarities between *D. silverstonei* and *D. trivittatus* are worth emphasis, particularly since the nominal *Hyla nigerrima* Spix—regarded as a synonym of *trivittatus*—is the generic type species.

The widespread Amazonian and Guayanan *Dendrobates trivittatus* (fig. 14) is as large or larger a frog than *D. silverstonei*, and it has about the same build, foot structure, and skin

FIG. 14. *Dendrobates trivittatus*, showing variation in color pattern; specimens arranged geographically from NE to SW, over air-line distance of about 2700 km. *Top*: AMNH 90923 from Airstrip Lely Mountains, 680 m., Surinam. *Middle*: AMNH 101564 from Pebas, 100 m., on Amazon River, Loreto, Peru. *Bottom*: AMNH 91840 from near Tingo María, about 700 m., Huánuco, Peru. Approximately ×1.2-1.3.

[1] A pattern of metallic dorsolateral stripes (not extending into groin), on a black ground, probably is synapomorphic for *Phyllobates* and, at the same time, is symplesiomorphic *within* the genus, being retained even in the ontogeny of *Phyllobates terribilis*, the species most derived in its coloration (Myers, Daly, and Malkin, 1978, fig. 3). The pattern is also reasonably predicted to occur in young *P. bicolor* and is retained by adults of the remaining species (*op. cit.*, pp. 329-330).

texture. As already discussed, *D. trivittatus* and *D. silverstonei* also have similar habits, and their calls are nearly identical (cf., figs. 10B, 10C). There are differences too: *Dendrobates silverstonei* is more primitive in retaining teeth, and perhaps also in its relative lack of muscle pigmentation, but its color pattern is more derived. Both species produce piperidine-based alkaloids, but the emphasis is on compounds of the pumiliotoxin-A class in *silverstonei* and on histrionicotoxins in *trivittatus*; there are no shared alkaloids. The taxonomic distribution of dendrobatid toxins having a piperidine base is more complex than that of the biosynthetically unrelated batrachotoxins, and analysis is deferred until completion of the sampling program (Daly et al., 1978; Myers, Daly, and Malkin, 1978, pp. 332-333). But it might be noted that the biochemical differences between *silverstonei* and *trivittatus* are similar to those between *Dendrobates histrionicus* and its possible daughter species *D. lehmanni* (Myers and Daly, 1976a, pp. 223-224, 243-244).

Excluding an autapomorphic, hence relatively uninformative, color pattern, and presently unassessed biochemical differences, *Dendrobates silverstonei* more closely resembles *D. trivittatus* than any other species familiar to us. Some portion of this resemblance doubtless will prove to be due to symplesiomorphy, once evolutionary polarity has been determined for various characters, but we suspect that some characters (e.g., the retarded trill call) may be synapomorphic. Therefore, we tentatively place *D. silverstonei* in Silverstone's (1976, p. 45) *trivittatus* species group. We have not yet had field experience with *D. bassleri*, the one other species presently in this group. *Dendrobates bassleri* shares at least one plesiomorphic character-state each with *silverstonei* (teeth) and *trivittatus* (striped color pattern). Since the apomorphic, or derived, condition is in each case confined to a single species (within this group), there presently is no further basis for assessing degree of relationship among the three species.

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